Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area

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AUTHORSHIP: SG, PRB, JMV, FL, TK, CDA, RF and ASJ conceived and designed the study. SG collected data and performed statistical analyses. DCL, JK, GB and NK contributed data. SG, PRB, JMV, FL, TK, CDA, RF and ASJ wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Accepted for publication in *Ecology Letters* published by Wiley-Blackwell

DATA ACCESSIBILITY: Should the manuscript be accepted, all relevant data would be archived in the Dryad public repository.

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Running title: Tree mortality across biomes

Keywords: Climate change, die-off, forest dynamics, functional traits.

Type of article: Reviews and Syntheses

Number of: Words in abstract: 200, Main text: 6714, References: 158, Figures: 6, Tables: 2

Abstract

Drought events are increasing globally, and reports of consequent forest mortality are widespread. However, due to a lack of a quantitative global synthesis, it is still not clear whether drought-induced mortality rates differ among global biomes and whether functional traits influence the risk of drought-induced mortality. To address these uncertainties, we performed a global meta-analysis of 58 studies of drought-induced forest mortality. Mortality rates were modelled as a function of drought, temperature, biomes, phylogenetic and functional groups, and functional traits. We identified a consistent global-scale response, where mortality increased with drought severity (log mortality (trees trees^{-1} year^{-1}) increased 0.46 (95% CI=0.2-0.7) with one SPEI unit drought intensity). We found no significant differences in the magnitude of the response depending on forest biomes or between angiosperms and gymnosperms or evergreen and deciduous tree species. Functional traits explained some of the variation in drought responses between species (i.e. increased from 30

to 37% when wood density and specific leaf area were included). Tree species with denser wood and lower specific leaf area showed lower mortality responses. Our results illustrate the value of functional traits for understanding patterns of drought-induced tree mortality and suggest that mortality could become increasingly widespread in the future.

INTRODUCTION

Increased frequency and intensity of drought events, defined as deviation from local long-term average climate, are predicted to occur throughout the world as a consequence of global climate change (Dai, 2013; Trenberth et al. 2014). Forest mortality related to extreme drought has already been reported worldwide (Allen et al. 2010, 2015), with potentially far-reaching impacts on forest diversity and function (Slik, 2004), human society and economies (Anderegg et al. 2013; Hanewinkel et al. 2013), biogeochemical cycling (Bonan 2008; Adams et al. 2010), and species distribution (Benito-Garzon et al. 2013). Forests play a major role in driving global climate due to their key role in hydrological cycling (Bonan 2008; Frank et al. 2015) and ability to sequester and store large amounts of carbon (Pan et al. 2011). Evidence already exists for a widespread reduction in carbon sequestration during drought in tropical (Gatti et al. 2014; Doughty et al. 2015) and temperate forest ecosystems (Anderegg et al. 2015).

There are many examples of drought-induced tree mortality, and several reviews and region-specific syntheses (e.g. Fensham et al. 2009; Allen et al. 2010; Phillips et al. 2010). Additionally, the information gleaned from observational studies of drought-induced tree mortality is supplemented by broad-scale experimental work, which usually allows clearer attribution of causes and deeper mechanistic understanding (Estiarte et al. 2016; Meir et al.

2015). There is however, a lack of quantitative synthesis at a global scale. Despite recent syntheses addressing size-dependent mortality (Bennett et al. 2015) and the importance of hydraulic traits in global-scale mortality (Anderegg et al. 2016), it is difficult to discern broad-scale patterns or to predict future responses. While differential mortality is often reported between co-existing species (e.g. Mueller et al. 2005; Ruthrof et al. 2015), and studies have increased our understanding of the physiological mechanisms of tree mortality (Mencuccini et al. 2015; Davi and Cailleret, 2017), there is still a lack of knowledge of drought-induced mortality responses of different tree functional strategies at a global scale.

Examples of recent mortality related to drought and heat stress exist across all forested continents and major forest types (Figure 1). In Northern temperate forests, high mortality rates are reported for *Pinus sylvestris,* associated with droughts in the 1990s and 2000s (Dobbertin et al. 2005; Galiano et al. 2010) and for *Populus tremuloides* in western Canada (Hogg et al. 2008) and in the USA (Worrall et al. 2008; Ganey and Vojta, 2011; Kane et al. 2014). Drought impacts are particularly well known in the Southwest USA (Allen et al. 2015), with high mortality of numerous tree species, including: *Juniperis monosperma* (Gitlin et al. 2006), *Pinus ponderosa*, *Pinus edulis, Pseudotsuga menziesii,* and *Abies concolor* (Ganey and Vojta 2011; Kane et al. 2014). Mortality is also well documented in Mediterranean areas, for example in Spain, high mortality is occurring in *Pinus halepensis* plantations (Garciá de la Serrana et al. 2015), in natural forests in the Sierra Nevada (Herrero et al. 2013) and in Scots pine populations in the Pyrenees and the north east (Vilà-Cabrera et al. 2013). In the southern hemisphere, broad-scale tree die-off events are affecting multiple *Eucalyptus* and *Corymbia* species in Australia (Fensham and Holman, 1999; Rice et al. 2004; Fensham et al. 2009; Matusick et al. 2013) and *Nothofagus* and *Austrocedrus* stands in Patagonia (Suarez and Kitzberger 2008). In tropical areas, extreme droughts associated with

El Niño-Southern Oscillation events have led to increased mortality in species-rich tropical forests in Asia (Aiba and Kitayama, 2002), Central America (Chazdon et al. 2005) and South America (Williamson et al. 2000) while 2005 and 2010 droughts in Amazonia were also associated with mortality increases (Phillips et al. 2009; Feldpausch et al. 2016).

Some studies suggest that drought and/or increased temperature impacts on demography will be greatest in, or limited to, already arid ecosystems (Ruiz-Benito et al. 2014). Indeed, a synthesis by Anderegg et al. (2015) found evidence of stronger reductions in tree growth after drought in dry ecosystems. Conversely, we could expect that the trees in these drier ecosystems may be more adapted to water stress (Arndt et al. 2015), and that the species growing in generally moister conditions could be most sensitive to extreme drought events (Jump et al. in press). Similarly, individuals growing nearer the dry range edge of their species may be more sensitive, but not necessarily, as local adaptation could play a role in counteracting the effects of drier conditions (Lázaro-Nogal et al. 2016). Current uncertainty about which areas are likely to be the most vulnerable to drought is an obstacle for conservation and management planning, while gaps in our understanding of the physiological explanations for drought-induced mortality, and high variation between locations and species make long-term and broad-scale predictions of forest vulnerability and community composition difficult (McDowell et al. 2013; Meir et al. 2015).

Drought-induced tree mortality can lead to long-term changes in the composition and structure of forests due to species and age-specific sensitivities (Martínez-Vilalta and Lloret, 2016). Cailleret et al. (2013) predict future broad-scale mortality of the dominant tree species *Picea abies* and *Abies alba* and their replacement with *Fagus sylvatica* in response to summer droughts in Bavaria, and Ruthrof et al. (2015) show that *Eucalyptus marginata* is more

sensitive to drought than *Corymbia calophylla* in southwestern Australia and predict future compositional shifts. Several examples exist where high mortality of dominant tree species suggests a shift in community composition; montane forests of Switzerland and northern Spain may be undergoing a vegetation shift due to increased drought. *Pinus sylvestris* suffers high mortality and poor regeneration and tends to be replaced by the more drought tolerant *Quercus* species (Galiano et al. 2010; Rigling et al. 2013; Aguade et al. 2015). In the Southwest USA *Pinus edulis* suffers high mortality during drought and *Juniperus* spp are becoming dominant (Mueller et al. 2005), or forest die-off leads to a persistent shift of vegetation type from forest to woodland (Allen and Breshears, 1998). In Patagonia, severe drought events have led to a shift in forest composition, with *Nothofagus dombeyi* being replaced with *Austrocedrus chilensis* (Suarez and Kitzberger, 2008). In extreme cases, changes in drought conditions could potentially lead to a biome shift, resulting in, for example, a seasonally dry tropical forest becoming a savanna, especially when other drivers of change, such as deforestation, act in synergy with drought (Staal et al. 2015).

Changes in tree species and functional composition directly affect forest structure and functioning, although today there is still debate on which functional groups are the most sensitive to drought. Functional groups are composed of individuals with shared physiological responses to, and impacts on, the environment (Tilman et al. 1997). Individuals are often classified into groups based on shared values of particular traits, with the aim of aiding the prediction of response to changes in environment (Hooper and Vitousek, 1997). Evidence exists for differential response of species depending on functional traits and groups; e.g. Phillips et al. (2010) found a higher sensitivity to drought in larger trees with lower-density wood in tropical forests. The functional composition of these forests is, therefore, expected to shift in favour of smaller trees with denser wood, which could result in a

159 reduction in carbon storage (Stephenson et al. 2014; Fauset et al. 2015). The study of changes
160 in functional composition, and the differential response of species depending on functional
161 traits or broad functional groups, could offer some scope for generalisation of drought
162 response and the mechanisms involved. Indeed, differences in response have been identified
163 based on broad taxonomic and functional groupings; for example, gymnosperms are
164 generally shown to be more sensitive to drought than angiosperms (Anderegg et al. 2015). In
165 Mediterranean and temperate regions of Europe, angiosperms and gymnosperms show
166 contrasting responses to global change. While drying climate reduces growth in both, an
167 increase in temperature and changes in recent management have been associated with
168 increased dominance of angiosperms at the expense of gymnosperms (Gómez-Aparicio et al.
169 2011; Coll et al. 2013; Rigling et al 2013; Vayreda et al. 2016). Widespread evidence also
170 exists that larger trees generally may be more at risk from drought-induced mortality (Phillips
171 et al. 2010; Bennett et al. 2015; McDowell and Allen, 2015). The importance of tree size has
172 been suggested in both observational studies and broad-scale experiments in tropical forests
173 (Nepstad et al. 2007; Rowland et al. 2015). Other traits implicated in drought responses, such
174 as wood density (Pratt et al. 2007), specific leaf area (Valladares and Sánchez-Gómez 2006)
175 and root depth (Irvine et al. 2002, 2004) also are likely to affect tree sensitivity to drought.
176
177 Given the likely impacts of climate change on ecosystem composition and function,
178 there is an urgent need to synthesise data on tree mortality in order to better understand
179 current patterns and predict the impacts on different forest biomes at a global scale. Here we
180 synthesised data from 58 papers including 398 tree species, from 33 locations and 42 drought
181 events worldwide (Figure 1). We modelled mortality data (proportion of standing dead trees
182 and annual rates) in response to drought and temperature, and we explored differences
183 between biomes and functional groups and investigated the influence of specific functional

traits. Specifically, we ask: 1) Is there a consistent broad-scale relationship between drought, temperature and forest mortality, or are there significant differences between biomes? 2) Are there differences in mortality based on major phylogenetic or functional groups such as angiosperms/gymnosperms or deciduous/evergreen species? 3) Do functional traits explain variation in species-level mortality?

METHODS

A global dataset of forest mortality in response to drought

We sought relevant peer-reviewed publications via Web of Science, Google Scholar and Scopus using combinations of the following search terms: "mortality", "drought", "forest", "tree", "dieback", "die-off", "defoliation", "drying" and "climate change". Additional references from the review of Allen et al. (2010) were also included. We screened papers for relevance based on the abstract and saved them for further consideration if they met the general criteria of reporting drought-induced tree mortality. Papers were selected for final inclusion in the meta-analysis if they met the following criteria: 1) mortality data were provided, as a proportion of trees dead, either as a single value based on one survey or as an annualized rate calculated between two or more survey periods; these two types of data were analysed separately. 2) Surveys were ground-based, from aerial photographs or satellite imagery, or a combination of these methods. 3) Mortality was attributed to drought (either one event or a series of events). Experimental studies were only included when the control plots were subject to natural drought during the experimental period and then only the data from these controls were included. 4) The data were collected at the plot level, with a minimum plot size of 0.01 ha, and a minimum number of trees for each species and plot of

five individuals. 5) The survey year(s) and the drought year(s) were clearly reported. 6) Cases where mortality occurred due to fire acting in combination with drought were excluded, but studies where biotic interactions such as attack by bark beetles had occurred were included. Finally, 7) mortality was reported for adult trees (not seedlings or saplings) at the species level. Initially, we studied more than 200 drought and mortality relevant papers in detail, and extracted relevant data. Finally, 58 papers met all the inclusion criteria, 30 of these provide annualized mortality rates, and 28 have single survey proportional values of standing mortality. The case studies cover all forested continents and major forest types (Figure 1). Thirty-three different locations (at the geographic scale of country or state in the case of USA) and 42 drought events (location/time combinations) are covered by our dataset. Selection criteria and particularly the need for quantitative mortality information led to several important and broad-scale studies being excluded (e.g. Phillips et al. 2009).

From each publication, we extracted information on the standing proportional mortality (% dead trees of all trees of each species) or an annual rate of mortality ($m=1-(N_1/N_0)^{1/t}$, where N_0 and N_1 are the number of trees present at the beginning and end of the survey interval, t (Sheil et al. 1995)), at the species-level. We report this species-specific mortality as a proportion: trees trees^{-1} year $^{-1}$. We also recorded species identity, geographic coordinates, year of the drought, plot size (ha) and sample size (No. plots and trees). If the information was available, we recorded site data as stand density (No. trees ha^{-1}), soil descriptions (e.g. order/classification, depth, texture) and management history. While such site-specific differences will introduce additional variation into the response of trees to drought, these factors were rarely reported, and we could not incorporate them into the analysis. We were also unable to account for forest age or successional stage, as this was

rarely reported. Full information on all studies and species included in the analysis is available in Supporting Information (Appendix S1 and S2).

Drought, temperature and functional trait data at a global scale

In order to assess the relationship between climate change and mortality we collected drought and temperature data. We calculated drought with the Standardised Precipitation Evapotranspiration Index (SPEI), using the mean SPEI at a 12-month timescale, obtained from SPEIbase v.2.3 (2014) (http://hdl.handle.net/10261/104742). SPEI is a multi-scalar drought index available as a global gridded dataset at a spatial resolution of 0.5° and has advantages over other drought indices as it allows for the identification of drought at different temporal scales, whilst also being sensitive to changes in evaporative demand (Vicente-Serrano et al. 2010). It has weaknesses, in that soil properties are not accounted for so it does not include a measure of water extractability, but we chose it here based on the evidence that it outperforms other traditional indices such as PDSI (Palmer drought severity index) and SPI (standardised precipitation index) (Vicente-Serrano et al. 2010; Bachmair et al. 2015; Blauhut et al. 2016). SPEI is calculated based on the difference (*D*) between monthly precipitation and potential evapotranspiration (*D=P-PET*), with the *D* values aggregated at different timescales from 3 to 24 months, following a procedure whereby SPEI is expressed as a standardised index, with negative values indicating drought over the timescale considered, relative to median values for a long-term reference period. SPEI currently covers the period January 1901 to December 2014. We chose a 12-month period, as it should identify prolonged droughts, of significance for trees. For temperature, we used monthly data from CRUTEM4 dataset (HadCRUT4, https://crudata.uea.ac.uk/cru/data/temperature/), a global gridded dataset at 0.5° spatial resolution (Osborn and Jones, 2014) developed by the Climatic

Research Unit (University of East Anglia) and the Hadley Centre (UK Met Office). For each study the climate data described above were extracted for the reported geographical coordinates for seven temporal windows: each of 1-5 years preceding the final date of mortality data collection reported in the study, the period between surveys (only for annual rate data), and the reported drought periods. Mean and minimum values of SPEI and mean and maximum values for temperature were calculated from monthly data for each of these periods for every study. We considered the SPEI for up to 5 years before the mortality occurred because a lag is often reported between drought and subsequent mortality. Although these climatic datasets are excellent resources for our global analysis, the somewhat coarse spatial resolution at which they are available potentially reduces the variation that we can explain since we are unable to consistently describe climate at a finer site-specific scale.

Each study was categorised into a broad biome type based on geographic location, species composition, climate conditions and forest type. Biome types are broadly based on the categories described by Whittaker (1975). We categorised each study to one of the following types: temperate gymnosperm (mid-high latitude and/or altitude forests composed mainly of gymnosperm species); temperate angiosperm (mid-high latitude and/or altitude forests composed mainly of angiosperm species); Mediterranean and dry woodlands (Mediterranean systems and dry temperate, subtropical woodlands and woodland savanna ecotones); tropical (wet tropical forests). While these biome categories encompass diverse forest types, alternative groupings did not lead to different results when the effect of biome was modelled. We obtained information on phylogenetic groups depending on angiosperm or gymnosperm classification and functional groups depending on leaf phenology/lifespan (evergreen/deciduous) by searching the literature for species information in peer reviewed publications. We obtained functional trait data from the TRY traits database (wood density

(WD), specific leaf area (leaf area per unit dry mass; SLA), maximum tree height (MH) (Kattge et al. 2011; Appendix S2)) and from the Royal Botanic Gardens Kew Seed Information Database (seed mass; SM: Royal Botanic Gardens Kew, 2016)). Full trait data was available for 171 of the 398 species in our dataset (see Appendix S2 for species list and data). The subset of species for which trait data were available was similar in terms of the balance between biomes to the full annual mortality dataset (Appendix S3, Table S3.1). For a small number of species, the trait value was extrapolated from the genus level, by averaging the value for three or more species of the same genus (details in Appendix S2). We selected the traits WD, SLA, MH and SM to achieve a balance between drought relevance and data availability. These traits are widely recognised as key traits of plant function and performance; they are relevant to growth, survival and reproduction and can determine species positions along major axes of ecological strategies of resource acquisition and use (Swenson et al. 2012; Díaz et al. 2016). Traits such as P50 (the xylem pressure inducing 50% loss of conductivity; Choat et al. 2012) may be more directly related to drought but hydraulic traits were not available for most species. We show the relationship between WD and SLA and raw mortality (Fig. S3.1 and S3.2 in Appendix S3) and P50 (Figure S3.3). For the species we modelled, we found a weak positive correlation between P50 and WD ($r = 0.2$), and a stronger positive correlation between P50 and SLA ($r = 0.75$ for a logarithmic fit; Figure S3.3). While the TRY traits database represents an excellent resource, we acknowledge that there are limitations associated with the application of species mean values. Variation in study methods, and differences in sample sizes between species occur for traits deposited in TRY, which could lead to some uncertainty around trait values, and there is no consideration of intraspecific variation. Nevertheless, we do not expect such variability to introduce a systematic bias into our analyses.

Statistical analysis

We followed a linear, three-step modelling process whereby we determined the effects on species-specific tree mortality of: 1) different timescales of SPEI and temperature; 2) biome and phylogenetic and functional groups; and 3) functional traits. We fitted linear mixed effect models using a normal error distribution and log link following an Information Theoretic Approach (Burnham and Anderson, 2002), where models are ranked based on AIC (Akaike Information Criterion) values. Models were fitted with the lme4 package (Bates et al. 2015) in R 3.2.2 (R Core Team 2015). Annualised and proportional species-level mortality data were log transformed prior to analysis, and were analysed separately due to the different nature of these data types. Since there were some zero values in the dataset, 0.001 was added to every mortality value before transformation.

To be sure of the representativeness of the timescale selected, we determined the effects of different timescales of SPEI and temperature on species-level mortality rate. Mortality was modelled against mean and minimum SPEI and mean and maximum temperature calculated at the seven timescales defined (each of 1-5 years before final mortality data collection, year(s) of reported drought, the years between surveys). The predictor variables were standardised to z scores prior to modelling using the scale function in R, which subtracts the mean and divides by the standard deviation. Models containing different combinations of the timescales of SPEI and temperature were compared with the best model selected through ranking of AICc values (AIC corrected for small sample size, Burnham and Anderson 2004; Bunnefeld and Phillimore 2012), and the importance of fixed effects was assessed through the magnitude of parameter estimates. We consider a reduction of AICc of 2 or more to indicate a significantly better model (Burnham and Anderson, 2004).

Additionally, a likelihood ratio test was performed to test the significance of the best model (as indicated by AICc value) compared to a null model containing only random effects, and the next best model in the AICc ranking. SPEI and temperature variables were included as fixed effects in all models, and a study-specific identifier was included as a random intercept to account for multiple species occurring in one study and for the site-specific information such as tree density and soil information that we were unable to include in the models. The different timescales of drought were investigated first through model comparison parameterised only with SPEI, and then temperature was added as an additional fixed effect to the model including the optimum drought timescale.

Once the most parsimonious combination of climatic fixed effects was determined, the differences between biomes and due to major phylogenetic and functional groups were investigated (i.e. angiosperms/gymnosperms and deciduous/evergreen, respectively). Biome was included as a fixed main effect and angiosperm/gymnosperm, deciduous/evergreen groups were included as a fixed main effect and an interaction term with climate (SPEI and temperature). Each model was compared to the same model without the inclusion of the respective subgrouping, based on model AICc values and likelihood ratio test.

Finally, the effects of functional traits on drought-induced mortality rates were determined. The four continuous functional traits (specific leaf area, maximum height, wood density and seed mass) were added to the best model identified through the process described above as both fixed effects and fixed effect interactions with climate. All traits were initially included and were sequentially removed based on parameter estimates, model AICc values and likelihood ratio tests, as described above. Prior to analysis, we checked for correlation and collinearity between traits. No pair of traits was significantly correlated (maximum r of

0.15 for WD and SLA) or collinear (maximum variance inflation factor (VIF; Dormann et al. 2012) of 1.2). We also used PCA to investigate trait collinearity and to determine if any combination of traits represented a certain functional strategy. No consistent strategies were identified (Table S3.2, Appendix 3). Trait data were standardised to z scores before modelling to allow parameter estimates to be compared. These functional trait models were fitted based on a subset of the data for which the functional trait data were available (171 of 398 species), so AICc values are not comparable with the full optimum model.

To better explore the direction of the important trait interaction effects identified through the above modelling process, predicted values based on models including each trait individually were plotted as 3D surface plots. These 3D plots were created in SigmaPlot (SigmaPlot v. 12.5 Systat software, San Jose); all other plots were created in R 3.2.2. (R Core team 2015).

RESULTS

The available standing proportional mortality data are based on single surveys and are limited in their value because it is not possible to determine the date of death, since the trees standing dead at one point in time may have died over a wide range of dates. Therefore, only the results from the analysis of annualised data, which could be attributed to specific drought events, are presented here. However, the results of this analysis were largely consistent with those for standing proportional mortality. The results for standing proportional mortality data, which were analysed separately, are available in Appendix S4.

Annualised mortality data consisted of 30 studies, 308 species and 27 drought events (Figure 1; Appendix S1). Drought intensity of the reported drought event was highest in Arizona in 2000-2004 with a SPEI value of -3.3 (a monthly mean value; Negron et al. 2009) and lowest in Costa Rica at -0.8 in 1997-1998 (Chazdon et al. 2005). Annual mortality rates (species-level) varied between 0.4 trees $trees^{-1}$ yr^{-1} (Negron et al. 2009) and zero (various sources).

Relationship between mortality, drought intensity and temperature

The observed SPEI values for the studies included in our analysis show some divergence from global values. A comparison of the distribution of SPEI associated with the study areas and mortality events, relative to the global values over the full time period covered by the studies (1977-2014), shows more negative SPEI values for the time periods associated with reported mortality events (the 5 years before final mortality surveys). There is, however, a large degree of overlap in the distributions of SPEI for the study period and the five years preceding the reported mortality event (Appendix S5).

The mean SPEI of the reported drought years was the best climatic predictor of annual mortality (Table 1). We identified a consistent response to drought that occurred across all biomes, with mortality increasing as values of SPEI decreased, i.e. as drought, defined as deviation from a long term mean, became more intense (Figure 2a, b). There is little support for the inclusion of biome as a fixed interaction with drought (ΔAICc = 3.2) and the parameter estimates for biome comparisons suggests that the difference in mortality between biomes is small (Figure 3).

Functional groups, phylogenetic groups and functional trait effects on drought-induced tree mortality

We detected no significant difference in the response to drought between angiosperms and gymnosperms or deciduous and evergreen species. The inclusion of these groups as fixed-effect interaction terms with SPEI did not improve the model (AICc increased by 0.2 and 0.7, respectively) and parameter estimates suggest no difference in drought mortality response (Figure 4a, b).

The functional traits WD and SLA influenced the drought-induced mortality response; the inclusion of these traits improved the model compared to one that included drought effects alone (Table 2; Figure 5a, b). However, MH and SM did not correlate with drought responses (Table 2). Drought-induced mortality was higher among species with lower values of WD (Figure 6a) and higher values of SLA (Figure 6b). We observed that the slope of interaction with WD was highest at very negative values of SPEI (more severe drought). For the interaction with SLA it is stronger at higher values of SPEI, (i.e. when drought is less severe), and the relationship is reversed compared to that seen at more negative values of SPEI, where mortality is slightly lower when SLA is higher (Figure 6b).

DISCUSSION

Global-scale patterns of drought-induced mortality

We found a consistent response of tree mortality to drought across biomes, indicative of a global-scale threat to forests from drought, which is consistent with the widespread nature of

recent reports of forest mortality (e.g. Allen et al. 2010, 2015). The fact that we find evidence for a linear increase in log (mortality) (Figures 2 and 5a) with increasing drought intensity means that the relationship with SPEI is exponential and, therefore, increases in drought could have critical consequences for forests. This result is indicative of a threshold response, and contrasts with other broad-scale studies that have suggested a linear relationship between mortality and drought (e.g. Phillips et al 2010). Such a response at the species-level seems realistic, given what we know of responses to drought intensity in individual studies (e.g. Meir et al. 2015). Note, however, that the shape of the drought-mortality response is likely to differ depending on the metric used to characterize drought intensity.

Our study is the first to identify a global-scale effect of drought intensity on tree mortality at the species-level; previous syntheses have either been limited geographically (Fensham et al. 2009; Phillips et al. 2010), or have focused on drivers such as size-dependence of mortality (Bennett et al. 2015) and the influence of hydraulic traits (Anderegg et al. 2016), rather than global patterns. It has been suggested that only dry forests are at risk from drought-induced mortality (Steinkamp and Hickler, 2015). Studies of tree growth have shown responses to drought occurring across the northern hemisphere, although with differences in timescale of response depending on long-term average aridity (Vicente-Serrano et al. 2014). Recent work provides a physiological basis for this global-scale vulnerability to drought-induced mortality, indicating that some 70% of forest species operate at narrow hydraulic safety margins irrespective of biome (Choat et al. 2012). Therefore, species in both arid and mesic habitats could be at high risk of embolism and related mortality if drought increases.

Our synthesis suggests that there is little difference between angiosperms and gymnosperms or between evergreen and deciduous species in the response of mortality to

drought, in line with a recent synthesis by Anderegg et al. (2016). Our global-scale analysis complements that of Anderegg et al. (2016) as these authors use a strict meta-analytic approach by comparing species within a study and consider hydraulic traits, while we focus on a range of traits that are more available and have broad applicability because they relate to multiple aspects of plant functioning (Díaz et al. 2016). We also account explicitly for drought intensity through the inclusion of SPEI data in our models. The fact that we obtain some common results, despite the different methods applied, gives increased support to both analyses. Although our selection of traits allowed for a large sample size, given the greater availability of data, there are certain drawbacks to consider, as the traits we study are unlikely to be directly related to drought-mortality responses. The use of traits with a stronger mechanistic basis (e.g., hydraulic traits) for which the relationship with drought-induced mortality is more direct is probably preferable when they are available.

While the global scale of our study is valuable for identifying broad-scale patterns, we acknowledge that the range of species and biomes included may have led to a masking of differences between groups, since in some cases the advantages of one functional strategy in one biome may not be applicable in another. For example, to be an evergreen species has different implications in temperate *versus* tropical forests. Furthermore, the small sample size and associated statistical limited power also may have constrained our ability to find differences between biomes and functional and phylogenetic groups. Despite these potential limitations, the global patterns that we identify and their congruence with related work by other authors demonstrates the value of this work for increasing our understanding of forest drought risk worldwide.

Functional traits mediate drought response

Our results suggest that high wood density can be associated with lower susceptibility to drought. Although wood density is a complex trait that may be associated with many ecological signals (Broderson, 2016; Gleason et al. 2016) this finding is substantially in accordance with reported functionality of this trait. Wood properties correlated with density affect water storage and transport, because the width and length of conduits determines hydraulic conductance (Chave et al. 2009) and wood density affects mechanical stability and is associated with resistance to drought-induced cavitation (Hacke et al. 2001; Pratt et al. 2007). In a study of saplings and seedlings from dry tropical forest, Markesteijn et al. (2011) found a lower vulnerability to cavitation (an ability to withstand more negative P50) in species with higher wood density. They also found evidence for a trade-off between cavitation resistance and hydraulic conductivity, suggesting that the ability to withstand drought leads to a competitive disadvantage during times when water is not limiting. However, weak support was found for this trade-off in a global synthesis by Gleason et al. (2016), which showed that many species can have both low hydraulic conductivity and low cavitation resistance, and that high wood density is not necessarily associated with low conductivity and high cavitation resistance. Generally, species with high wood density are associated with lower growth rates and lower background mortality rates (Chave et al. 2009). The results of our study show that this strategy can lead to lower mortality rates when exposed to drought stress. In contrast to our findings, Hoffmann et al. (2011) found that although species with higher density wood had higher cavitation resistance, their mortality under drought was higher, due to an inability to prevent declines in water potential, compared to species with less dense wood. Hoffmann et al. studied the response to an especially severe drought at the community level, whereas we consider a wide range of drought conditions and vegetation types, suggesting that differences in overall drought severity and spatial scale

might explain the differences between the results that they report and those presented here. It is notable that despite the complexity of this trait and its relationship with hydraulic performance, we still find a significant, although noisy, global signal.

Our analyses provide evidence that tree species with high specific leaf area can be more susceptible to drought-induced mortality than species with lower specific leaf area, although the nature of the relationship varied with drought severity. Specific leaf area determines plant response to changing resource availability (i.e. water and light), photosynthetic potential and growth rates (Poorter et al. 2009). Depending on stomatal properties, higher specific leaf area could imply a higher potential for leaf water loss; in contrast, a low specific leaf area is often associated with xeromorphic plants, adapted to high water stress (Bussotti et al. 2015). Furthermore, woody species associated with arid niches are characterised by relatively lower specific leaf area in the Mediterranean (Costa-Saura et al. 2016). An experimental study by Valladares and Sánchez-Gomez (2006) showed within-species lower specific leaf area if seedlings were exposed to drought, although across species, a high specific leaf area was associated with greater drought tolerance. Reducing specific leaf area under prolonged drought conditions seems to be consistent across species and studies (Poorter et al. 2009) and is suggestive of a higher resistance to drought in plants with a lower specific leaf area. Although we identify a global-scale signal in the relationship between drought and SLA, as for wood density, many ecological signals are associated with SLA making this relationship highly complex. In the future, the integration of directly relevant traits such as P50 could improve the approach taken here.

Several studies have shown that larger trees could have lower resistance to drought (e.g. Bennett et al. 2015). For example, an experimental drought in a Brazilian Amazonian

rainforest resulted in much larger increases in the mortality rates of larger trees compared to smaller ones (Nepstad et al. 2007; Rowland et al. 2015) and a pan-tropical analysis also revealed that larger trees tend to suffer most during drought (Phillips et al. 2010). A global-scale synthesis by Bennett et al. (2015) shows that drought-related mortality is generally greater in larger trees; they analysed drought mortality related to DBH, but they hypothesised that the relationship is due to height effects. However, in our global-scale analysis that explicitly included species maximum height, we did not find a strong effect due to tree height. This apparent contrast might be because the importance of the other traits that we considered overwhelmed any effect of height, but it also could be due to the different approach taken in our study compared to that of Bennett et al. Our analysis was based on species-level maximum height, while their study used size classes at the plot level irrespective of species. Future work should seek to incorporate individual-level tree heights and stand age, as this will provide the most direct assessment on the importance of tree size.

Implications

Our results suggest that at a global scale, trees with lower wood density and higher specific leaf area tend to be more sensitive to drought. Future increases in the intensity and duration of drought events could therefore lead to changes in forest composition and structure, with implications for forest diversity and ecosystem function. Changes in functional diversity due to the drought sensitivity of different species will also affect forest functioning and drought resilience (Laureto et al. 2015). Forests are an important global carbon sink (Pan et al. 2011) and changes in forest energy exchange could have major consequences for global climate (Frank et al. 2015). Wood density and specific leaf area are both traits that are important for carbon sequestration (Prado-Junior et al. 2016) and storage in aboveground biomass (Chave

et al. 2014). It is, therefore, important to consider the impacts that the greater vulnerability associated with particular values of these traits under drought conditions could have on broad-scale carbon storage (Finegan et al. 2015). Generally, higher biomass might be expected to be stored in ecosystems rich in species with levels of these traits associated with high growth rates (low wood density and high SLA (Grime 1998)), but this is context dependent. For example, in dry tropical forests, species with high wood density and low specific leaf area are associated with high growth rates and carbon storage, precisely because they can continue to function during drought (Prado-Junior et al. 2016). Our results also have successional implications; early successional tree species are characterised by low wood density and high specific leaf area (Aiba et al. 2016). If disturbance increases due to drought-induced mortality, then these early successional species could dominate forests, making the community more susceptible to future die-off.

Our synthesis identifies global-scale drought-induced tree mortality responses, and our analyses of species-specific mortality rates with climate and functional trait data provide quantitative insights into global-scale patterns. However, our best model only explained 37% of the variation in mortality rate. To reliably assess the impact of drought events, and to predict the consequences for forests in the future, effective long-term monitoring across a wide range of forest types is required. In addition, detailed reporting of site conditions would allow future syntheses to consider the importance of factors such as tree density in drought-induced mortality at a global scale (Jump et al. in press). Here, we identified drought-induced mortality responses worldwide that are species-specific, but further analysis depending on stand and tree level characteristics are critical to adequately identify and manage vulnerable forests. Additionally, the consideration of intra-specific variation in functional traits could significantly improve our ability to predict the responses of forests to future drought. The

traits we have identified as critical for drought resistance at a global scale are known to vary within species across environmental gradients (Fajardo and Piper, 2011), thus trait variation across environmental gradients (e.g. Vilà-Cabrera et al. 2015) should be incorporated in future models to better predict climate change impacts in forests worldwide. Although our results do not have high predictive power in themselves, they provide an advance, since our current ability to predict drought-induced mortality is limited (Meir, Mencuccini and Dewar, 2015) and this prediction needs global assessment. Our study highlights the global vulnerability of forests to drought-induced tree mortality and shows that widely available functional traits, such as wood density and specific leaf area, can improve explanatory power.

Conclusion

Based on a synthesis of studies of drought-induced tree mortality events at a global scale we find evidence of greater forest mortality risk from more severe droughts, consistent across biomes and major functional groups. Using functional traits, we could explain an additional fraction of the variation in drought-induced tree mortality. Trees with less dense wood and high specific leaf area may be most at risk. These results further illustrate the value of species-level trait data for understanding general trends in species responses. Overall, our findings indicate that, with increasingly severe future droughts projected, associated drought-induced tree mortality could become increasingly widespread, with significant implications for forest diversity, ecosystem function and climate feedbacks.

ACKNOWLEDGEMENTS

This research was supported by The Leverhulme Trust via International Network grant IN-2013-004, together with the European Union Seventh Framework Programme under PCOFUND-GA-2010-267243 (Plant Fellows) co-funded by the University of Stirling. The study has been supported by the TRY initiative on plant traits (http://www.try-db.org). The

TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is/has been supported by DIVERSITAS, IGBP, the Global Land Project, the UK Natural Environment Research Council (NERC) through its program QUEST (Quantifying and Understanding the Earth System), the French Foundation for Biodiversity Research (FRB), and GIS "Climat, Environnement et Société" France. Support to CD Allen provided by the U.S. Geological Survey's Ecosystems and Climate & Land Use Change mission areas (through the Western Mountain Initiative). We also thank the following authors for kindly providing us with their original tree mortality data: Shin-Ichiro Aiba, Robin Chazdon, Joseph Ganey, Eric Gustafson and Íñigo Grazow de la Cerda. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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SUPPORTING INFORMATION

Appendix S1: Information on the studies and species included in the meta-analysis

Appendix S2: Species list, mean trait values, A/G and D/E classification and sources of trait data, including citations and details of the species for which data was extrapolated from the genus level.

Appendix S3: Trait data information: biome representation, raw mortality against traits, relationship between wood density and specific leaf area and P50, TRY trait reference list.

Appendix S4: Model results from single survey proportional mortality data analysis.

Appendix S5: SPEI distribution of study areas compared to global values over the same period.

TABLES

Table 1: Model comparison using AICc values (AIC corrected for small sample size) and parameter estimates for sets of models used to identify the optimum model(s). The 95% confidence intervals associated with the parameter estimates are shown for the fixed effects in the best model, highlighted in bold. SPEIm represents mean SPEI and TEMPm mean temperature. Confidence intervals were calculated with boot strapped resampling. The random effect included in these models was a study specific identifier. Results of likelihood ratio tests (P-values) are shown for the best models compared to the null model (one including only random effects) and the next best model, as indicated by AICc values.

Fixed effect(s)	**Parameter estimate(s) (95% CI)**	**AICc**	**ΔAICc**	**R^2 marginal/ conditional**	**P-value**
SPEIm drought years	**-0.46 (-0.7 to -0.2)**	**1876.7**	**0.0**	**0.06/0.29**	**0.0005; <0.0001**
SPEIm between survey years	-0.43	1880.1	3.4	0.05/0.32	
SPEIm drought + TEMPm 3 years pre survey end	-0.46; -0.01	1880.3	3.6	0.06/0.30	
SPEIm drought + TEMPm 5 years pre survey end	-0.46; 0.002	1880.3	3.6	0.06/0.30	

SPEIm drought + TEMPm 2 years pre survey end	-0.46; -0.007	1880.3	3.6	0.06/0.30
SPEIm drought + TEMPm 4 years pre survey end	-0.46; 0.0009	1880.3	3.6	0.06/0.30
SPEIm drought + TEMPm between survey years	-0.46; 0.01	1880.4	3.7	0.06/0.30
Min SPEI drought years	-0.45	1880.5	3.8	0.06/0.34
Min SPEI 2 years pre survey end	-0.54	1880.8	4.1	0.03/0.33
SPEIm + maximum temperature 2 years pre survey end	-0.46; -0.04	1880.8	4.1	0.06/0.30
SPEIm + maximum temperature 3 years pre survey end	-0.46; -0.01	1880.9	4.2	0.06/0.30
SPEIm + maximum temperature 4 years pre survey end	-0.45; 0.01	1880.9	4.2	0.06/0.30
SPEIm + maximum temperature 5 years pre survey end	-0.45; 0.01	1880.9	4.2	0.06/0.30
SPEIm drought + maximum temperature between survey years	-0.45; 0.009	1880.9	4.2	0.06/0.30
Minimum SPEI between	-0.39	1881.5	4.8	0.04/0.34

survey years				
Min SPEI 3 years pre survey end	-0.32	1883.0	6.3	0.03/0.33
Min SPEI 4 years pre survey end	-0.30	1883.3	6.6	0.03/0.32
Min SPEI 5 years pre survey end	-0.31	1883.3	6.6	0.03/0.33
SPEIm 2 years pre survey end	-0.24	1883.8	7.1	0.02/0.31
SPEIm 3 years pre survey end	-0.27	1884.3	7.6	0.02/0.30
SPEIm 5 years pre survey end	-0.19	1885.8	9.1	0.01/0.31
SPEIm 4 years pre survey end	-0.15	1887.0	10.3	0.006/0.31

Table 2: Model comparison and selection when considering functional traits and drought response. AICc values (AIC corrected for small sample size) and parameter estimates for sets of models used to identify the optimum model. SPEIm represents mean SPEI. The model containing the best combination of fixed effects is shown in bold. The traits considered are wood density (WD), specific leaf area (SLA), maximum height (MH) and seed mass (SM). The results of likelihood ratio tests are shown for the best model (P-value), compared to a null and the next best model. Here the null model for comparison contains random effects and the fixed effect of mean SPEI of the drought.

Fixed effect(s)	**Parameter estimate(s)**	**AICc**	**ΔAICc**	**R^2 marginal/conditional**	**P-value**
SPEIm drought + SPEIm drought x WD + SPEIm Drought x SLA	**-1.28 (-2.04 to -0.52) 0.38 (-0.2 to 0.97) -0.41 (-0.95 to 0.13)**	**1013.5**	**0.0**	**0.14/0.37**	**0.001; 0.01**
SPEIm drought + SPEIm drought x WD	-1.19; 0.39	1014.8	1.3	0.10/0.33	
SPEIm drought + SPEIm drought x SLA	-1.22; -0.38	1015.7	2.2	0.09/0.34	
SPEIm drought	-1.14	1016.6	3.1	0.06/0.30	

SPEIm drought + SPEIm drought x WD + SPEIm drought x MH	-1.26; 0.26; -0.63	1016.6	3.1	
SPEIm drought + SPEIm drought x WD + SPEIm drought x SLA + SPEIm drought x MH	-1.28; 0.27; -0.26; -0.53	1016.8	3.3	0.15/0.37
SPEIm drought + SPEIm drought x SLA + SPEIm drought x MH	-1.24; -0.22; -0.56	1019.7	6.2	0.10/0.33
SPEIm drought + SPEIm drought x (WD, SLA, MH, SM)	-1.28; 0.37; -0.27; -0.5; -0.21	1022.8	9.3	0.16/0.38
SPEIm drought + SPEIm drought x SM	-1.17; -0.12; 0.02	1022.9	9.4	0.07/0.31

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FIGURES

Figure 1: Locations of the studies included in the analysis. Dark grey shading indicates studies providing annual rates of mortality based on two or more surveys and light grey standing proportional mortality values based on a single survey (these are analysed separately with annual mortality rate analyses presented in the main text and single survey proportions presented in supporting information). The biome category of each study is indicated by shape. Temperate gymnosperms: diamonds, temperate angiosperms: triangles, Mediterranean and dry woodlands: circles and tropical: squares. Annual mortality studies: Aiba and Kitayama, 2002; Chazdon et al. 2005; Condit et al 1995; da Costa et al. 2010; Dobbertin et al. 2005; Faber-Langendeon and Tester 1993; Fan et al 2012; Ganey and Vojta 2011; Granzow de la Cerda et al. 2012; Gu et al 2015; Hogg et al. 2008; Huang et al. 2010; Itoh et al. 2012; Kane et al. 2014; Kardol et al. 2010; Klos et al. 2009; Kukowski et al. 2013; Mueller et al. 2005; Nakagawa et al. 2000; Negron et al. 2009; Newbery and Lingenfelder 2008; Olano and Palmer, 2003; Potts, 2003; Poulos, 2014; Smith et al. 2015; Tafangenyasha, 1997; Tsopelas, 2001; Tsopelas et al. 2004; van Nieuwstadt and Shiel, 2005; Worall et al. 2008. Single survey proportional mortality studies: Aakala et al. 2011; Becker et al. 1998; Bowker et al. 2012; Cailleret et al. 2013; Fensham, 1998; Fensham and Holman, 1999; Floyd et al. 2009; Foden et al. 2007; Garcia de la Serrana et al. 2015; Gitlin et al. 2006; Heitzman et al. 2007; Khan et al. 1994; Koepke et al. 2010; Linares et al. 2011; Lwanga, 2003; Markalas, 1992; Martínez Vilalta and Pinol, 2002; Matusick et al. 2013; Millar et al. 2012; Mokria et al. 2015; Rice et al. 2004; Savage, 1997; Slik, 2004; Suarez and Kitzberger, 2008; Twidwell et al. 2014; Viljoen, 1995; Vincke et al. 2010; Zegler et a. 2012.

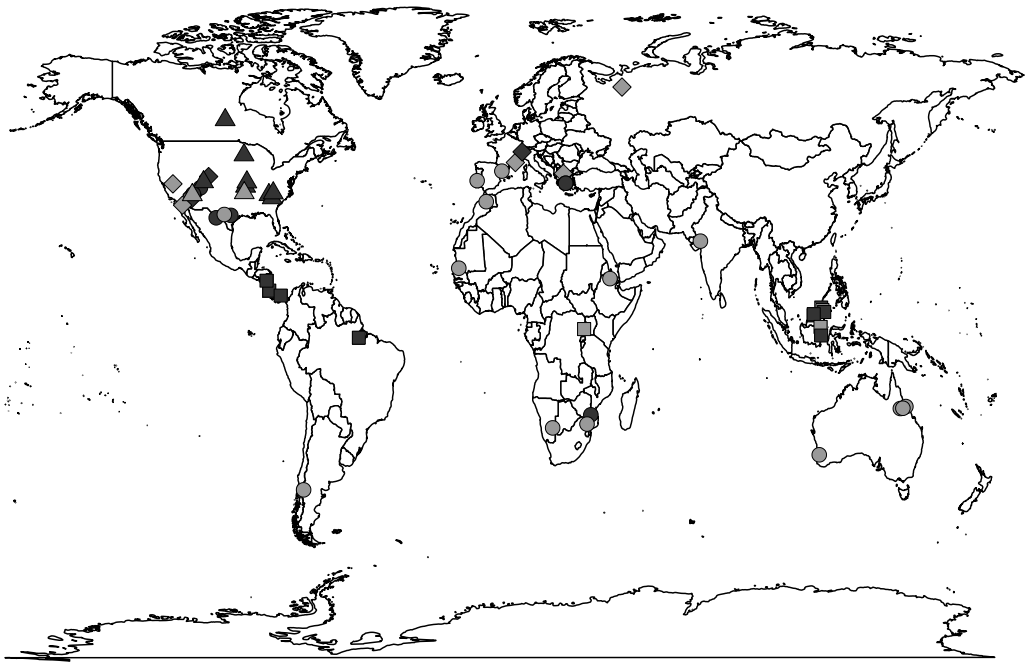
Figure 2: Annual observed mortality data at species-level plotted against mean SPEI for the reported drought years (a), and log-scale annual observed mortality against mean SPEI for the reported drought year, including the model prediction using the parameter estimate for the best model with 95% confidence intervals (b). More negative values of SPEI indicate more severe drought.

Figure 3: Parameter estimates for the model including mean SPEI of the reported drought years and biome as fixed effects to test if drought induced mortality varies by biome. The parameter estimates show the difference in the mortality response to drought of each biome with 95% confidence intervals, calculated using bootstrapped resampling. Sample sizes (number of studies) by biome are as follows: temperate gymnosperms: five, temperate angiosperms: eight, Mediterranean and dry woodlands: seven and tropical: ten.

Figure 4: Parameter estimates for the models including mean SPEI of the reported drought years and the groups angiosperms/gymnosperms (a) and evergreen/ deciduous (b) as fixed effect interactions with mean SPEI. 95% confidence intervals are shown, calculated using bootstrapped resampling.

Figure 5: Relationship between predicted annual mortality and drought (solid line) with 95 % confidence (dotted lines) based on the best model including the effect of climate and its interaction with species-level functional trait data (WD and SLA). This is based on a subset of the mortality data, for which trait information was available (a). Parameter estimates for each of the fixed effects included in the best trait model, with 95% confidence intervals, calculated using bootstrapped resampling (b).

Figure 6: The effect of the interaction of mean SPEI of the reported drought years with wood density (WD) (a) and specific leaf area (SLA) (b) on log drought-induced tree mortality (trees trees $^{-1}$ year $^{-1}$).



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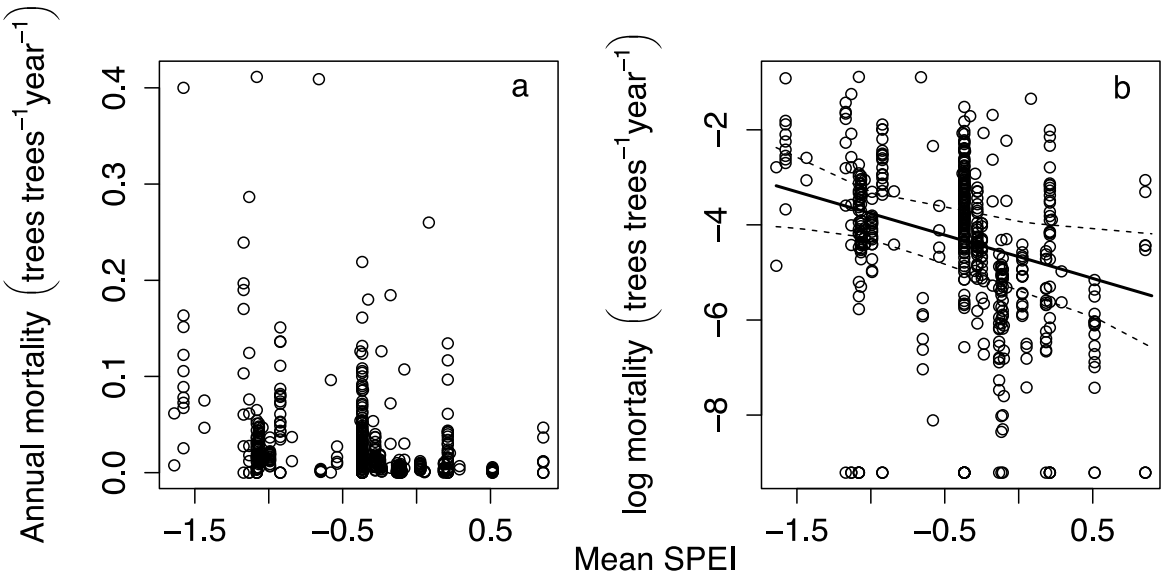
1320 **Figure 1**



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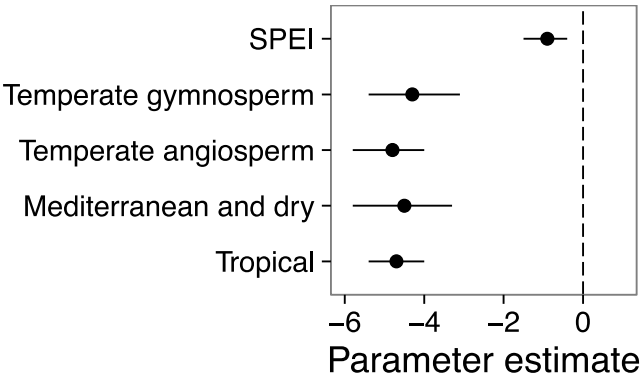
1322 **Figure 2**



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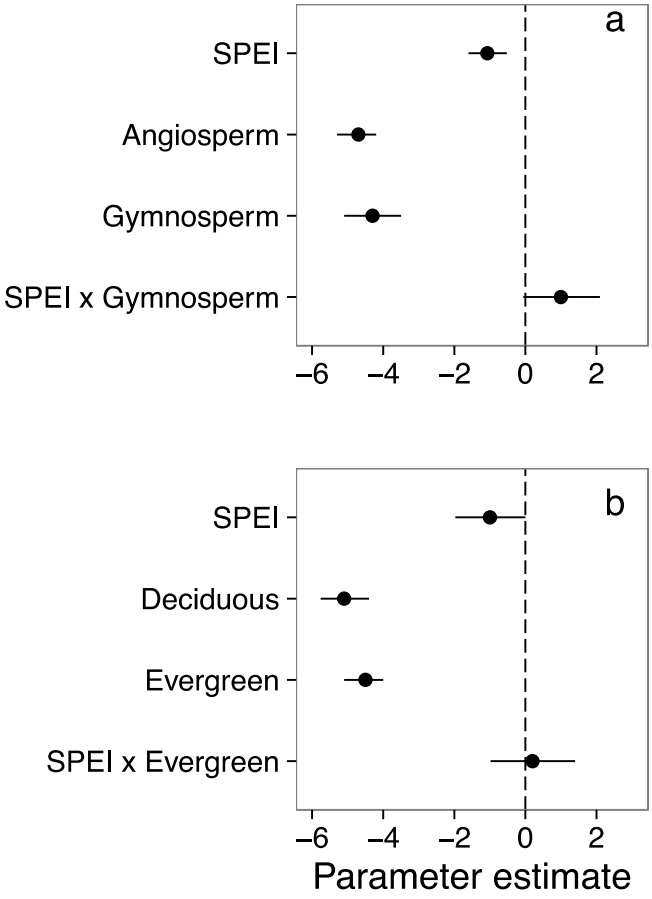
1324 **Figure 3**



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1326 **Figure 4**

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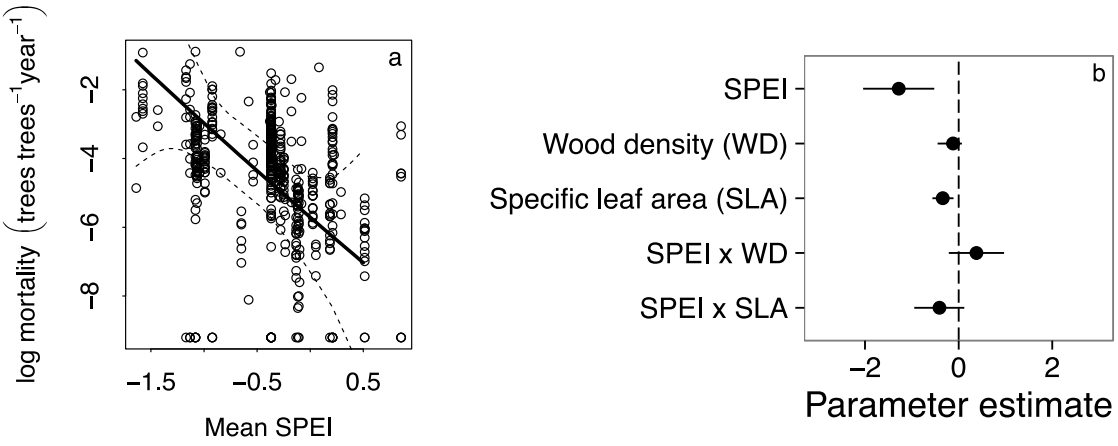

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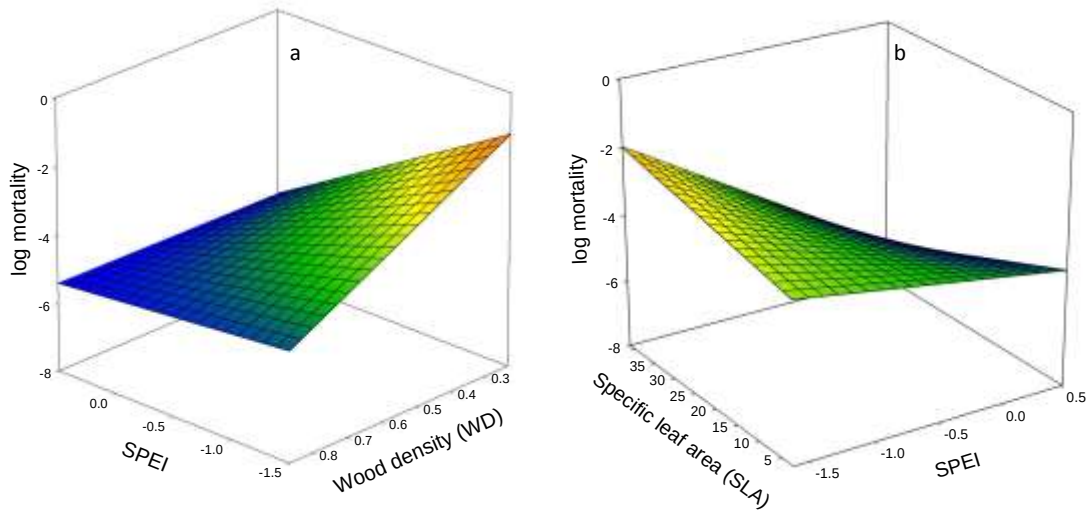
1330 **Figure 5**



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1332 **Figure 6**

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